

Larval habitats and life history of the Crete Island endemic *Boyeria cretensis* (Odonata: Aeshnidae)

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Key words: Odonata, dragonfly, *Boyeria cretensis*, life cycle, spatial distribution.

ABSTRACT

Boyeria cretensis belongs to the most threatened European dragonfly species. It is restricted to some isolated permanent streams on the island of Crete. The streams have a pronounced gallery vegetation and are situated in a narrow belt of altitude between 50 and 400 m. We understand very little about the biology of this species so information is required to develop effective conservation measures. The life cycle and spatial distribution of the larvae were studied at a small perennial stream in the central part of Crete during three consecutive years. The larvae showed a preference for calcareous sinter mineral substrate associated with organic material such as roots, leaves and wood. This microhabitat selection is supposed to be mainly an antidrift strategy, since *B. cretensis* lives in habitats with a dynamic hydrology during the rainy period in winter. On the other hand, it may also be a strategy to avoid predation from fish and crabs. The last seven larval stadia were determined by wing sheath length and head width. Based on data of head width frequency distributions, a univoltine or semivoltine life cycle is discussed.

INTRODUCTION

It is well known that species endemic to islands are often threatened. This is due to a high level of isolation, small population sizes (MacArthur & Wilson 1967), and, in some cases, rapid environmental shifts on small island ecosystems. Therefore it is not surprising that about half of the 'critically endangered', and also the only two 'extinct' dragonfly species on the global Red List of threatened species are island endemics (IUCN 2007). For instance 10 species of Hawaiian Odonata are considered to be critically endangered or extinct, all of which are endemics belonging to the genus *Megalagrion* (Polhemus 2004). More than 45% of the species of Sri Lanka are endemics with a high number of threatened species (Bedjanić 2004). Other examples of 'critically endangered' endemics were also recorded from the Comoros, the Seychelles and the Mascarenes (Clausnitzer 2006; Clausnitzer & Martens 2004).

Species of the Aegean archipelago in the Mediterranean are threatened due to recent climatic change and human impact on their ecosystems. The most important factor is the increasing lack of water on the islands. Two species, *Coenagrion intermedium* Lohmann and *Boyeria cretensis* Peters, are endemic to the island of Crete. *B. cretensis* was described as late as 1991 (Peters 1991). Previously *Boyeria* in Crete was as-

sumed to be a disjunct eastern island population of the western counterpart *B. irene* Fonscolombe. Only a few suitable habitats are known to be breeding sites for *B. cretensis* (Fig. 1), whereas *C. intermedium* is common across the whole island. The distribution of the former is restricted to shady mountain streams, with permanent water and pronounced gallery vegetation, in a narrow belt of altitude between 50 and 400 m belonging to the thermomediterranean and mesomediterranean zone of the island (Jahn & Schönfelder 1995). Due to the small range of distribution and the high level of stenotopy *B. cretensis* is one of the most threatened European dragonfly species. It is classified as 'vulnerable' on the IUCN Red List of threatened species (Müller 2006). It is inexplicable that the species is not listed by the European Fauna-Flora-Habitat directive (Sahlén et al. 2004).

Several observations on the imagines (Schneider & Müller 2006) and some data on the distribution range of *B. cretensis* (Lopau 2000) are available, however little is known about the biology of the larvae, for instance life cycle, spatial distribution and microhabitat. Schneider & Müller (2006) emphasized that further knowledge of its habitat requirements is necessary to develop effective conservation measures for this endangered endemic species. From 2004 to 2006 I studied a population of *B. cretensis* in a stream of the Ida Mountains. My aim was to investigate the spatial distribution of the larvae and to obtain information on the life cycle.

MATERIAL AND METHODS

Study area

The investigation was carried out at the Mili River S of Rethimno in the central part of Crete Island (Fig. 1). The Mili River was a small mountain rivulet in the north-western mountain range of the Ida Mountains. The stream originated from a rocky formation at ca 600 m above sea level. The study site was situated at a stretch of 100 m altitude difference below the spring of the stream near the village Miloi (Mili). It had permanent running water all year and passed a narrow steep-sided valley well shaded by trees (*Quercus*, *Acer*, *Platanus*, *Ficus*, *Laurus*, *Nerium*, and *Ceratonia* spp.). At the study site the valley was 20-100 m wide and the slopes of the valley reached up 50-100 m. In most stretches the river flew irregularly over stones, gravel, or a cover of detritus. The water level was between 5 cm at waterfalls and 0.2-0.5 m along normal flowing river stretches, which were 0.5-2.0 m in width. There were also rock pools (Fig. 2) with a depth between 0.5 and 1.5 m. The flow rates varied depending on the backwater in the pools and the width of the river. At the waterfalls a flow rate of ca 200 l·min⁻¹ was measured during the visits in late spring, summer and early autumn. Drift lines along the river banks indicated a high flood level with a depth of approximately greater than 2.5 m during the rainy season in winter. Between spring and summer the water temperature varied between 16°C and 20°C at ambient air temperatures, to around a maximum of 35°C outside the valley. Most stretches of the river were completely shaded with only a few sunspots. No aquatic plants were present in the sampled riverbed.

Besides *Boyeria cretensis* larvae, imagines of five odonate species were recorded at the stream: *Calopteryx splendens cretensis* Pongracz, *Coenagrion intermedium*, *Ischnura elegans ebneri* Schmidt, *Orthetrum brunneum* (Fonscolombe), and *O. coerulescens anceps* (Schneider). The most abundant species in this river section were *C. intermedium* and *I. elegans ebneri* among the Zygoptera, and *B. cretensis* among the Anisoptera. Several other benthic macroinvertebrates were associated with this

odonate assemblage, e.g., *Baëtis vernus*, *B. sp.*, *Cloëon dipterum*, *Electrogena sp.* (Ephemeroptera); *Leuctra sp.* (Plecoptera); *Beraea pullata*, *Hydropsyche sp.*, *Polycentropus sp.*, Psychomyiidae gen. sp., *Tinodes unicolor* (Trichoptera); *Gerris spp.*, *Notonecta maculata*, *Velia sp.* (Heteroptera); Chironomidae gen. sp., Limoniidae gen. sp., Tipulidae gen. sp. (Diptera); *Graptodytes veterator*, *Gyrinus urinator*, *Laccophilus hyalinus*, *Nebriporus sp.* (Coleoptera); and *Potamon potamios* (Crustacea). The stream contained no fish at the sampling site but fish were present in the lower stretches of the river (V. Driyannakis pers. comm.).

Larval sampling and measurements

The sampling site had a length of 350 m and included all common structures of the river bed. Altogether 38 m² of the riverbed was investigated. Larvae were caught using a pentagonal handnet with a maximum width of 30 cm (mesh size 1 mm, wooden handle 1 m). This handnet was particularly useful for sampling larvae in layers of coarse detritus and between tufts of submerged roots. Additionally a hand-sieve (30 cm in diameter, mesh size 1 mm) was used for sampling in shallow water bodies and in submerged caves, treeholes, and coarse gravel. The field work was carried out during the following dates: 5-10 July 2004, 8-12 October 2004, 5-8 October 2005 and 17-20 April 2006.

For larval sampling the river was surveyed in an upstream direction. Larvae of all size-classes were removed from short stream sections (5 m) and measured for total body length, head width and length of the right hind wing sheath using a sliding caliper and an optical measuring device (both 0.01 mm). After measuring all larvae were released at the sample sites. The location of each larva and the quality of substratum in its microhabitat were recorded. Additionally, in July 2004 and October 2004/2005, all exuviae of the ultimate stadium were collected. Although monthly data for one complete year were not available, the data of several years in combination with phenology and emergence data allowed initial conclusions of voltinism of *B. cretensis* in this stream.

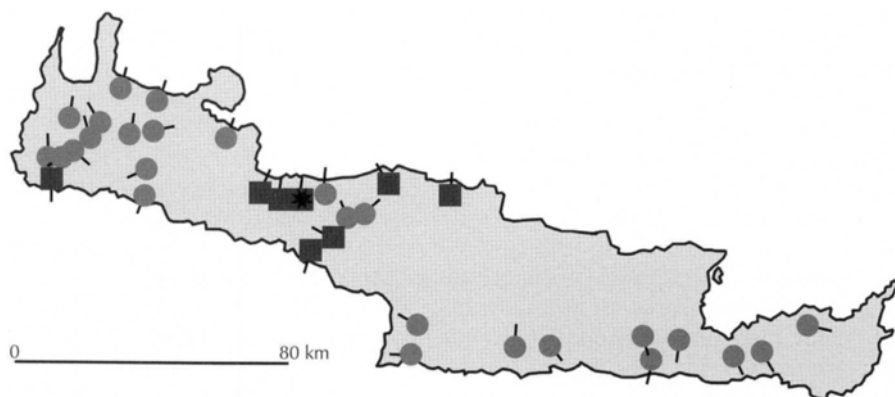


Figure 1: Distribution of permanent running waters in Crete Island — (circles) potential habitats of *Boyeria cretensis* before the 1970s (Malicky 1977) but without recent occurrence of the species; (squares) larval populations of *B. cretensis* detected from 1990 to 2006 (Lopau 2000; Schneider & Müller 2006). The flow direction of all waters is indicated by a short bar. The study site is marked by an asterisk. It is unlikely that all streams mapped in the 1970s are still perennial.

Statistical analysis

The types of substrate were classified into six categories: (I) leaves above gravel ($n = 23$); (II) leaves above calcareous sinter ($n = 15$); (III) calcareous sinter, covered with roots and leaves ($n = 16$); (IV) rotten wood and leaves cemented with sinter ($n = 8$); (V) roots ($n = 15$); (VI) roots associated with leaves ($n = 14$). In each category a different number of samples were available because the substrate types had varying frequencies in the river bed. ANOVA was used to analyse the relationship between substrate types and species abundance, with the substrate type as the factor and the density of individuals per m^2 in each substrate type as the response variable. To compare species abundance within pairs of substrate types an a posteriori analysis was performed using the Tukey/Kramer test. All calculations were run with SPSS.

RESULTS

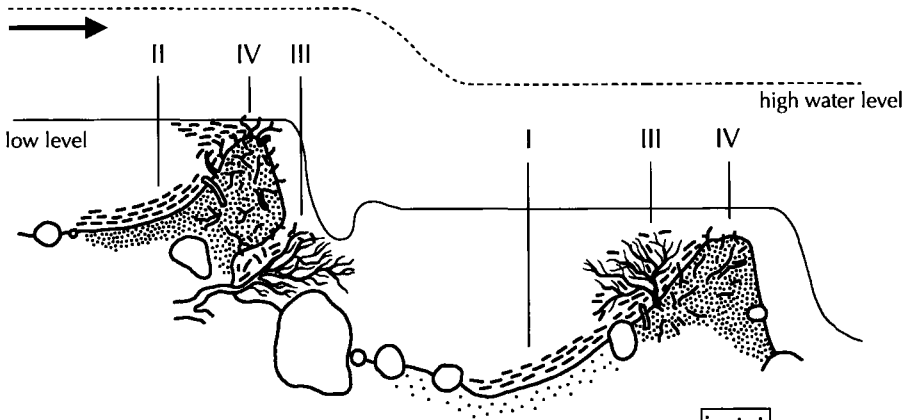
Larval microhabitat

In the Mili River *Boyeria cretensis* larvae of all stages were mainly recorded in stretches located between waterfalls characterized by different kinds of substrates. A cross section, as well as a longitudinal section, of typical river stretches indicating sites where the larvae were caught is depicted in Figure 3. Besides calcareous sinter, small sand and gravel banks, pebbles and rocks, and a variety of organic substrata were also found. Layers of coarse detritus – mainly rotten leaves and wood – and



Figure 2: Typical section of the Mili River where *Boyeria cretensis* was investigated.

a



b

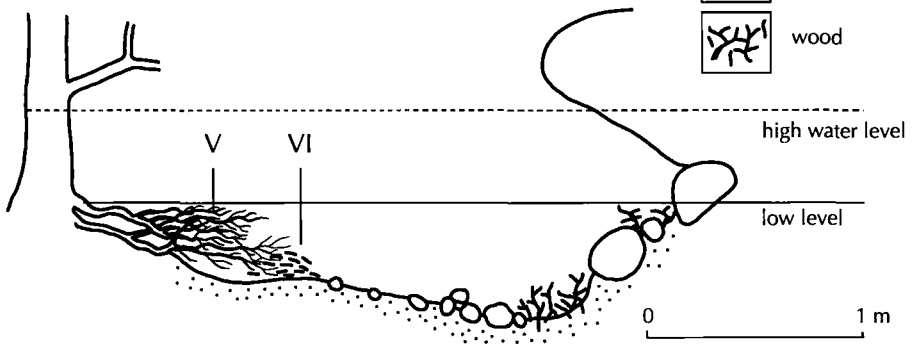


Figure 3: Microhabitats in the bed of the Mili River — (a) longitudinal section of two waterfalls with a rocky pool; and (b) cross-section of a normal permanent stretch. The numbers I-VI indicate the microhabitat structures shown in Figure 4.

submerged roots from the trees were the most frequent and conspicuous habitat structures in these stream sections. Only a few larvae were found in stretches where the river bed consisted only of rocks, sand and gravel. In all years larvae were found in the same substrate types in similar proportions.

Among all investigated microhabitat structures 42% of the larvae were collected on calcareous sinter that was associated with and covered by roots and leaves (Fig. 4). In contrast, only 2% of the larvae inhabited the layers of rotten leaves above the calcareous sinter. In leaves situated above gravel the proportion of larvae found was 24%. The difference in abundance between the substrate types was highly significant (ANOVA; $p < 0.001$; $F_{5,85} = 4.708$). The pairwise comparisons of the Tukey/Kramer test indicated significant differences ($p < 0.05$) in abundance between substrata I and III, and II and III. Larvae inhabited substrata IV, V, and VI in similar densities of ca 10 individuals per m^2 (Fig. 4). No significant differences were found between abundance in rotten organic material cemented with calcareous sinter (mainly located at the waterfalls), pure roots (V), and leaves held on by roots (VI). Most larvae were found living well camouflaged between particles of detritus and threads of roots. They were never found buried in sand or fine detritus. In two cases single larger larvae were found in small submerged treeholes.

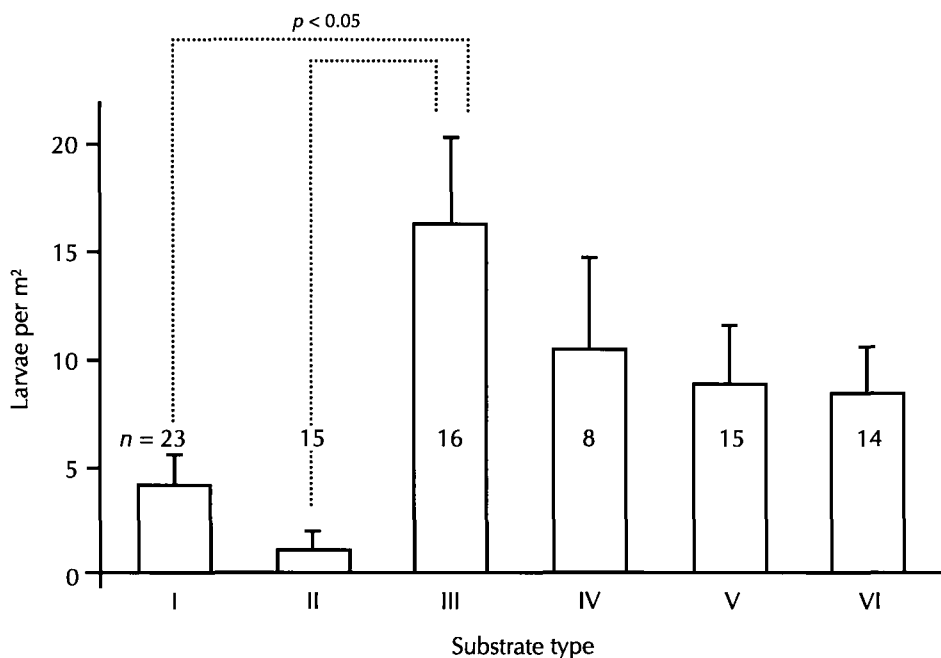


Figure 4: Density of *Boyeria cretensis* larvae [individuals per m^2] found in different microhabitats — (I) leaves above gravel; (II) leaves above sinter; (III) sinter covered with roots and leaves; (IV) rotten wood and leaves cemented with sinter; (V) roots; (VI) roots associated with leaves. Dotted lines indicate significant differences in the abundances between substrata I and III, and II and III (Tukey/Kramer test; $p < 0.05$).

The current speed at the larval microhabitats ranged from 0 to 20 cm·s⁻¹. The water depth at the larval microhabitats ranged from less than 5 mm at the overfalls of small waterfalls and in treeholes at the water surface, up to 1.5 m in the deep rocky pools.

Voltinism

Seven distinct stadia could be separated by plotting the length of the wing sheaths against head width (Fig. 5). The data include a total of 266 individuals from samples collected from all sites. Both parameters increased stepwise at each moult. This allowed assignment of each larva to a certain stadium. The composition of larval population for four different months during the study period is depicted in Figure 6. In July 2004, only individuals of the stadia F-6 and F were recorded ($n = 18$). All final stadium larvae indicate the emergence period. Besides these F larvae, more than 60 exuviae were found on the rocks and vegetation along the river that had hatched days and weeks before. In October 2004 ($n = 136$) the F-3 stadium was most abundant followed by F-5, F-4, and F-2. Only a small number of F-1 larvae and no F larvae were found. Also younger larvae < F-5 were not recorded in October 2004. A similar pattern occurred in October 2005 except for the presence of a small number of F-6 larvae. The peak of F-3 larvae in October shifted to F-1 stadium in April 2006. Furthermore a clear shift of size frequency was observed indicating development between autumn and spring, i.e. during winter.

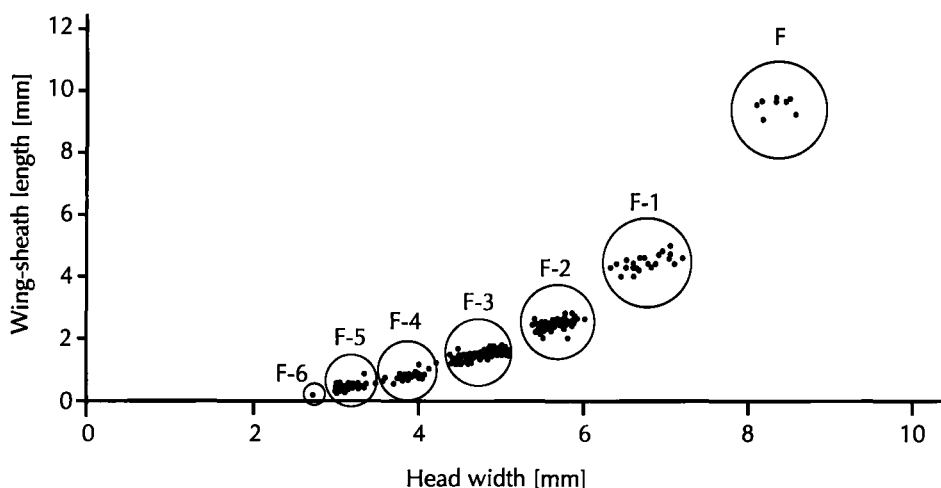


Figure 5: Scatterplot of size measurements of larval *Boyeria cretensis* ($n = 266$). The scatterplot of the wing sheath length against the head width separated seven different stadia (F-6 to F).

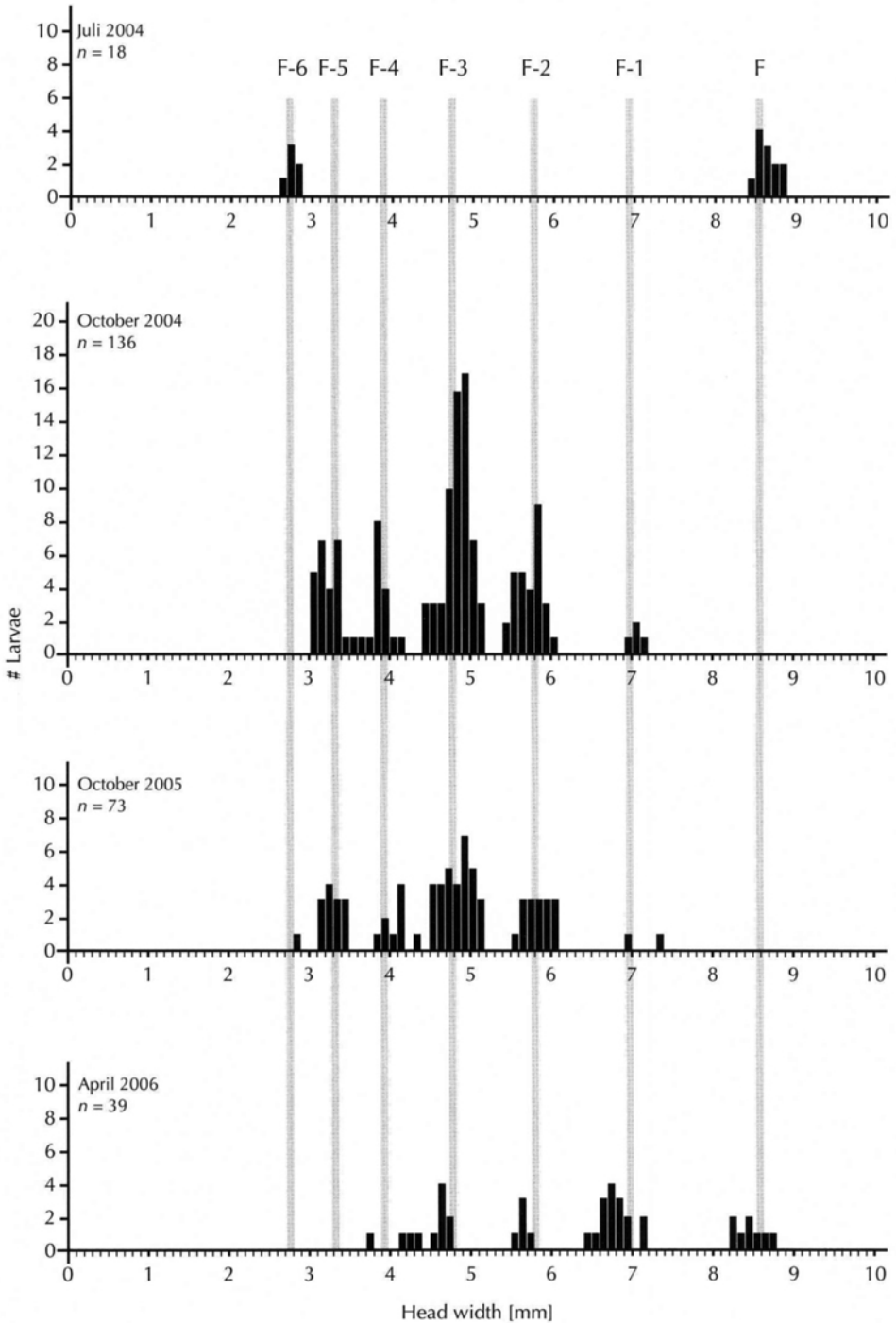


Figure 6: Size frequency diagramm of larval *Boyeria cretensis* over a period of two years.

DISCUSSION

In the Mili River *Boyeria cretensis* larvae show a preference for calcareous sinter mineral substrate associated with organic material such as roots, leaves and wood. Larvae have never been found on the open surfaces of stones or rocks and they also avoid the top of sandy substratum. Nevertheless the larvae prefer strong and stable substrates (Fig. 4) such as calcareous sinter covered with roots and leaves, rotten wood and leaves cemented with calcareous sinter, roots only, and roots associated with leaves. In early spring and during the rainy season in winter the Mili River is temporarily in flood (see water levels in Fig. 3). The preference for a specific stable microhabitat in this kind of rain-dependant river system may be an antidrift strategy. Furthermore the occupied microhabitats are an effective refuge against crab or fish predation. Odonate larvae are not very accessible for predation when hidden between plants and roots or under layers of detritus (Thompson 1987; Wellborn & Robinson 1987).

The substrate choice of *Boyeria* may generally depend on the most available substrate type giving shelter and, according to the literature, this can vary across *Boyeria* species and locality. In streams and rivers of southern France *B. irene* mainly occurs in tree roots (Leipelt & Suhling 2001). By contrast, Wildermuth (2005) found *B. irene* larvae under stones in stream sections with stony or rocky bottoms where organic substrates are sparse. The larvae of the North American *B. grafiana* Williamson, and *B. vinosa* Say also live under stones (Walker 1958), however, according to Phillips (1996) larvae of *B. vinosa* only live in woody debris. Furthermore, Worthen et al. (2001) reported that *B. vinosa* prefers river stretches with sandy river beds. Unfortunately information on microhabitat structures is limited. Whereas the American and European species of *Boyeria* are comparatively well investigated, less is known about the Asian species of the genus. The larva of *B. sinensis* Asahina is still unknown. *B. maclachlani* Selys inhabits small rivers in Japan. Larvae of this species have been caught mainly in between woody debris and roots (F. Suhling pers. comm.). Ueyama et al. (2005) reported *B. maclachlani* larvae from sandy and muddy substrates but gave no information on their microhabitat.

In comparison with available data of the congeners, *B. cretensis* shows all features of a typical summer species sensu Corbet (1954) including a long flying season, lower synchronisation of emergence and a relatively elongated emergence period in the year. Imagines have been recorded between the end of May (R. Jödicke in Lopau 2000) and late October (Schneider & Müller 2006). Most imagines have been recorded between July and August (several records in Lopau 2000) when most dragonfly watchers visit Crete Island as tourists, therefore observations of imagines were recorded more frequently during this period. In the warm south of Crete Island the flying season may start already in late March or April as indicated by unconfirmed observations of adults (K. Westermann pers. comm.: 30 March 2005; OM unpubl.: 18 April 2006). It may be possible that different local populations show different population dynamics and phenology patterns in relation to water temperatures, e.g. at different altitudes and different climatic regions of the island. At the Mili River no imagines were found in April, and there was no full-grown larva, which would indicate emergence during this time. The main flying season is thought to be between July and October. Records of imagines indicate a long flying and egg laying season of more than four, or even five, months per year in this local population. However,

no data of the synchronisation rate during the emergence period are available. Nevertheless, the long flying season and the frequency of final stadium larvae in the July samples suggest that the synchronisation of emergence is generally low in a single local population or low between local populations of different river systems. In the valley of the Mili River at least half of the final stadium larvae had hatched by the first visit to the field site in early July 2004, indicated by exuviae that were found along the river. Mature imagines were also observed at the river during this time, patrolling and laying eggs (Schneider & Müller 2006). The last oviposition was observed on 5 October 2005. It is possible that the winter temperatures at the study site allow continuous egg development and growth of the larvae. A long egg laying period and the lack of a winter diapause could be the reason for a variable duration of larval development within one generation. A possible model of voltinism is shown in Figure 7.

As the egg laying period starts in June, the first-hatched larvae may reach the F-3 stage in October. By accepting the postulate of a continuous larval growth during winter, this part of the cohort may therefore reach the ultimate stadium in spring with adults emerging in late summer the following year. In this case a univoltine development is possible. However just a few small larvae were found in the spring samples and there is no doubt that they had hatched from eggs laid in September or October. This cohort grows up to the F-7, F-6 or F-5 stadium during the following summer and then spends the next winter in F-1 or the final stadium. The emergence of this cohort takes place in early summer and larval development is assumed to take two years within a semivoltine life cycle.

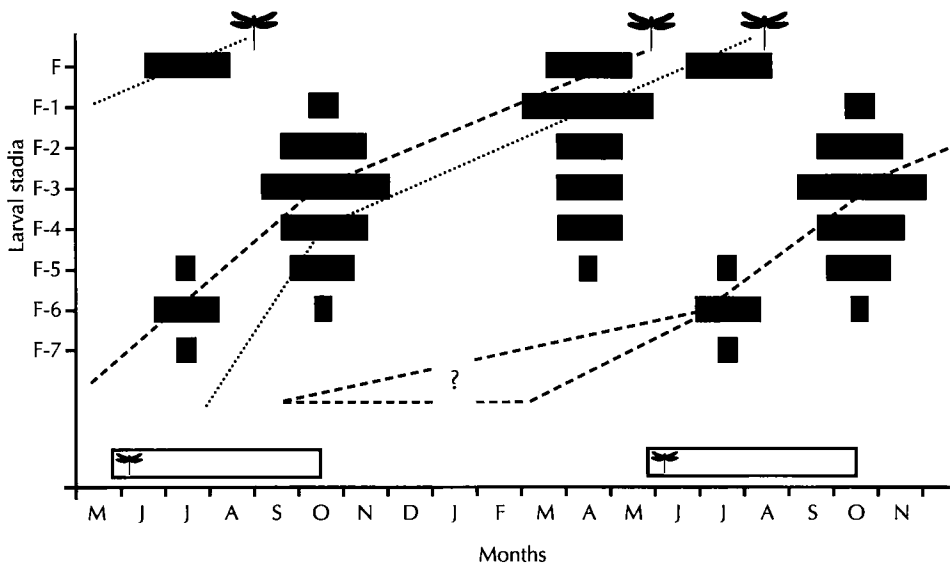


Figure 7: Model of voltinism of *Boyeria cretensis* — based on data sets on larval development and on adult phenology in three consecutive years. Black bars: relative number of individuals in each stadium; white bars: flying season; dashed line: semivoltine life cycle; dotted line: univoltine life cycle.

Comprehensive investigations have been published on voltinism in *B. irene*. According to Ferreras-Romero (1997) in the Sierra Morena Mountains (Andalusia, Spain) *B. irene* is semivoltine or occasionally partivoltine with few individuals requiring a maximum of three years to complete development. Wildermuth (2005) suggested that larvae mainly require two or three years to complete their development in southern France. *B. vinosa* in North and South Carolina is semivoltine (Paulson & Jenner 1971; Smock 1988). Galbreath & Hendricks (1992) recorded a univoltine life history at higher latitudes in Virginia but this assumption conflicts with the fact that higher latitudes normally correlate with increased time of larval development (Corbet 1999: 225; Corbet et al. 2006).

Freshwater habitats, especially permanent running waters, are very rare on the islands of the Aegean Sea and particularly on Crete Island. The most important factors that cause the lack of such biotopes are the dry regional climate, the low water capacity of the soil, and several human activities causing loss of vegetation and over-exploitation of freshwater resources. Crete has a high winter rainfall of 300-700 mm per year in the lower parts and up to 2,000 mm in the mountains (Malicky 1977). However, during the summer there is an extreme drought period lasting several months so most of the frequent running waters are non-permanent. The majority are ephemeral and totally dry during the long hot dry season between April and October. Nevertheless a small number of permanent running waters contain a rich and diverse aquatic freshwater fauna (Malicky 1977). This special biocenosis also contains dragonfly assemblages that include the two endemics *Coenagrion intermedium* and *B. cretensis*. The latter species shows a clear preference for shaded streams (Schneider & Müller 2006) and the current occurrence of this species may be limited to approximately a dozen streams on Crete. Thus, even without further human influence, *B. cretensis* is surely one of the most endangered dragonfly species in Europe (Sahlén et al. 2004). The effects of global climate change and, in particular, increasing water consumption for tourism and agriculture has direct influences on the destruction of the freshwater habitats of these rare local populations. Besides climatic effects, tourism along with the agricultural policy of the European Community (Beaufoy 2001) are reducing the survival chances of *B. cretensis* by changing the water regime of the rivulets and by the destruction of their gallery vegetation. The current Red List status 'vulnerable' (Müller 2006) may therefore be too optimistic. There is no doubt that this extremely rare species will not survive the potential downward spiral of these conditions in the future.

ACKNOWLEDGEMENTS

I would like to thank my wife Gerlind Müller for logistical support during field work. This manuscript was improved by comments from Frank Suhling, Andreas Martens and Bernd Kunz. Frank Suhling helped with the analysis. The species identification of the macrozoobenthos would have been impossible without the help of Lars Hendrich (Coleoptera) and Torsten Berger (all other taxa). I thank Bea Müller for reading an early version of the manuscript, Misa and Werner Piper for the translation of a Japanese paper, Vagelis Driyiannakis for his local support in the Mili gorge, and Sarah Yeates for the improvement of the language.

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